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THE NUTRITION OF THE EMBRYO SAC AND EMBRYO IN CERTAIN LABIATÆ, ... *F. H. Billings.*

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THE NUTRITION OF THE EMBRYO SAC AND EMBRYO IN CERTAIN LABIATÆ.

BY F. H. BILLINGS.

Plates XI to XIV.

SOON after the publication of a paper on seed development, in which various sympetalous families were considered, the writer began an investigation of embryo-sac nutrition as found in the Labiatæ. Literature upon the subject indicated the presence of certain nutritive structures that resembled some of those described in the paper mentioned above. The structures consisted of outgrowths or specialized portions of the embryo sac which by enlargement frequently replaced considerable portions of the integument. The position and shape of the structures are characteristic in some instances of the family in which they occur. It is therefore one of the problems of the present investigation to ascertain what degree of uniformity prevails among a number of genera of the Labiatæ, and thus determine, if possible, whether any special type of embryonic structure is liable to become characteristic of the family. Though the number of species studied is but a small representation of the total number distributed over the earth, still, as will presently be shown, a great enough similarity exists among them to warrant the supposition that a like resemblance probably exists among the remainder. It would not be safe to extend such a conclusion to any family taken at random, inasmuch as some families are aggregates of groups, such as subfamilies, which may not be closely allied phylogenetically but which are associated on account of fulfilling certain taxonomic requirements.

One of the services that may ultimately be performed for taxonomy is that of testing the homogeneity of families. The results could be reached satisfactorily only after all the species of any given family had been examined as to their ontogeny. Taxonomically speaking, the Labiatæ are regarded as a fairly homogeneous family with well-marked characteristics.

Species whose common ancestors are not remote should show similarity in embryonic particulars, since these are doubtless the ones least influenced by environment.

No attempt was made to work out the stages preceding fertilization in every instance. Several species were examined, however, and the series of events constituting the earlier history of embryo-sac development were found to be identical.

The ovular primordium gives rise to a single megaspore mother cell, from which originates an axial row of four potential megaspores. The most deeply seated of the four develops into the ordinary type of an eight-celled embryo sac.

The growth of the embryo was followed in detail in *Lamium amplexicaule*, and it was found that the various stages in development correspond closely to the plan observed in most dicotyledonous embryos. However, it is not with the development of the embryo but with the behavior of the embryo sac that this paper has most to do.

Many of the writings of early investigators who worked along embryological lines show that there was little thought of assigning physiological significance to peculiar shapes assumed by the embryo sac. More recently quite a number of observers have entered the field, and they have shown the wisdom of correlating morphology and physiology. Bibliographies of their papers have been published from time to time, so that only the literature cited in the text, or very recent papers, will be given here.

The single and unusually thick integument of many Sympetalæ, including the Labiatæ, appear to serve a double function. The outermost layers become transformed into a seed coat, while the inner or remainder, wholly or in part, may become a nutritive tissue (Nährgewebe) which invites, as it seems, the digestive and absorptive activity of the endosperm. Sometimes the nutritive tissue is more or less localized, as can be seen from the deposits of starch in certain regions. In other instances the deposition of food material is general throughout

the integument, so that no special part would be likely to become a particular point of attack by the endosperm.

When the absorptive activity of the endosperm is largely centered in some outgrowth or differentiated portion of the embryo sac, the term "haustorium" is applied to such a portion. In instances where haustoria are not developed, the digestive and absorptive power is more or less equally distributed over the entire surface of the embryo sac. Where absorption is going on most rapidly, the cells directly concerned in the appropriation of the nutritive material are usually abundantly supplied with plasmatic contents. In case of the presence of a haustorium the endosperm cells lying adjacent to the base of the haustorium show the greatest richness in plasmatic contents.

The following genera and species of Labiatæ form the bases of the detailed description:

Lamium amplexicaule.
Stachys palustris.
Phrysostegia virginiana.
Leonurus cardiaca.
Brunella vulgaris.
Teucrium canadense.
Pycnanthemum lanceolatum.
Lycopus rubellus.
Mentha canadensis.
Salvia lanceolata.
Salvia azurea.
Monarda fistulosa.
Nepeta cataria.
Dracocephalum sp.
Scutellaria parvula.

Lamium amplexicaule.

This species will be given more detailed consideration than the others, for it will serve in a measure as a type of the family and also as a basis of comparison for the other species. The embryo sac, at the time fertilization is accomplished, contains the usual form of egg apparatus (fig. 1). The endosperm nucleus is large, spherical in form, and contains a vesicular nucleolus. The nucleus does not lie near the egg apparatus, as is the case in so many plants, but at the opposite end of the sac near the disintegrating antipodals. The contour of the sac shows a constriction which may be used to distinguish a larger upper, or micropylar portion, in which the egg apparatus lies, from a smaller, lower, or antipodal portion, in which the endosperm nucleus lies. The endosperm nucleus does not leave the antipodal region, but immediately after fertilization develops a tissue in its end of the sac. Double fertilization probably occurs, though it was not observed.

The egg responds to fertilization by elongating greatly, and pushing down into the forming endosperm tissue (figs. 2, 3). The elongation is at first due to the growth of the entire egg cell. A transverse wall soon separates the suspensor from the proembryo. It is thus seen that the cell which is to develop into the embryo is removed altogether from the micropylar portion of the sac. For a time this portion contains no active nuclei, the synergids being in a process of disintegration. But endosperm nuclei soon migrate into it through the space lying between the suspensor and the wall of the embryo sac. The nuclei are but few in number and they do not form tissue (fig. 4). From this time on, the two extremities of the embryo sac are very sharply distinguished. The antipodal end is soon filled with a compact growing tissue that surrounds the embryo. Increase in size of the tissue takes place rapidly, so that the micropylar portion shortly becomes the smaller (fig. 4). A remnant of nucellus can usually be seen as a disorganized mass of cells lying at one side of the micropylar expansion of the sac. For a considerable length of time the endosperm tissue extends only to the constriction, beyond which lies the micropylar region with its wandering endosperm nuclei. An examination of the integument cells surrounding this region shows that dissolution is in progress—due, of course, to the predatory activity of this part of the sac. The antipodal portion, with its endosperm tissue, exerts a similar absorptive influence, but the material absorbed by the latter is retained or used up in building more tissue, while that absorbed by the former is not, but is transferred to the endosperm tissue. The micropylar portion of the embryo sac may therefore be regarded as a haustorium. Evidence of the results of haustorial activity is seen in the unusual richness of plasmatic contents in the endosperm cells bordering on the haustorium. The presence of starch in the basal portion points to the same conclusion.

The nuclei of the haustorium do not form tissue, as has already been stated. In *Lamium amplexicaule* they take no definite position. Although they have the same origin as the nuclei of the endosperm tissue they differ considerably from them. The chief difference lies in their much greater size. These may attain a length of over thirty micromillimeters, which is greater than the average diameter of an endosperm

cell (fig. 5). The haustorial nuclei vary usually from twenty to thirty micromillimeters in diameter, but the smallest are much larger than any formed in the endosperm tissue, since these average only about five micromillimeters in diameter. Another difference is the much greater size of the nucleoli of the haustorial nuclei. In addition, the nucleoli are not vesicular, as are most of those in the endosperm tissue, but are solid. The large size of the nucleoli would seem to indicate an increased nutritive function on the part of the nucleus, especially in light of the theory that nucleoli represent reserve food substance. There is no evidence that the haustorial nuclei undergo division, either in *Lamium* or in the cœnocytic haustoria of any other of the Labiatæ investigated. There is some variance in the explanations of the peculiarity of these nuclei, but discussion of them will be reserved till the close of the paper.

The suspensor elongates during the growth of the embryo sac and finally attains an unusual length (fig. 6). Its course is for some time plainly visible in the haustorium and for a longer time in endosperm tissue. The portion nearest the embryo persists while the remainder slowly disintegrates. The appearance of the suspensor is such that at no time does it seem to serve as a conductor of food substances to the embryo, at least from any locality other than that of the endosperm tissue immediately surrounding it. It appears to have fulfilled its function when it carried the embryo from the haustorium down into the midst of developing endosperm tissue.

While the micropylar haustorium is transferring materials to one end of the endosperm tissue the opposite end is nourished by substances conducted through a vascular bundle that passes down the integument and terminates near the chalaza. The little depression or pocket in which the antipodals undergo disintegration is deepened until it forms a short canal, which extends from the endosperm toward the terminus of the vascular bundle. It does not merit the name of haustorium to the extent that the micropylar expansion of the sac does, since it exerts little or no absorptive influence upon the integument cells bordering it, but rather seems designed to facilitate conduction from the bundle. Its increase in length is not accompanied by a pronounced increase in diameter nor does it contain nuclei.

Later stages in embryo development show increase of the

endosperm tissue and a consequent encroachment upon the haustoria. Just when the micropylar haustorium ceases to function is hard to say. Its activity probably does not cease as soon as it begins to be encroached upon by the endosperm tissue. The nuclei in fact remain till late stages in seed development.

Stachys palutris.

The embryo sac seen in figure 7 presents markedly differentiated portions. The stage shown here is reached in the same manner as a corresponding one in *Lamium.* While the endosperm is beginning its formation in the antipodal end of the sac a number of nuclei migrate into the haustorium. They distribute themselves over the micropylar end of the haustorium, where the cytoplasm is chiefly located. The opposite end is distinctly vacuolated. It will be noticed that the constriction is very narrow. Through it passes the suspensor with an enveloping layer of cytoplasm. The regions adjacent on each side of the constriction are stored with starch, the result evidently of the absorptive activity of the haustorium. As in *Lamium,* the cells of the endosperm tissue nearest the haustorium are richer in plasmatic contents than those at a distance.

The canal that conducts from the terminus of the vascular bundle is comparatively long in *Stachys.* It is sharply bent about midway in its course, one arm running longitudinally to connect with the end of the vascular bundle.

Stachys and *Lamium* vary in the structure of their embryo sacs only in minor details, the main difference being the more definitely placed haustorial nuclei in *Stachys.* The embryo is nourished in both by the endosperm tissue surrounding it, this in turn being assisted in its growth by the activity of the haustorium. It is probable that the suspensor does not function in the conduction of materials to the embryo, on account of the disorganized condition of its cells. The food materials gathered by the haustorium are transmitted to the endosperm tissue through that part of the constriction lying around the suspensor.

Phrysostegia virginica.

This species has a peculiar appearing embryo sac when the stage shown in figure 8 is reached. Such difference as may be noted, when it is compared with *Lamium* and *Stachys,* is due principally to the direction of growth taken by the endosperm

tissue. If the growth had been uniform in all directions the long axes of the haustorium and endosperm tissue would have been approximately parallel. In *Phrysostegia* the endosperm grows in a one-sided fashion, producing a bend in the embryo sac of about ninety degrees. The haustorium is a club-shaped sac containing a few large nuclei. Its upper or micropylar end is vacuolated, while its lower end, adjoining the endosperm tissue, is densely protoplasmic. The suspensor is exceedingly long.

The position of the antipodal canal is peculiar in this species. It is located near the haustorium—a situation explained by the short length of the vascular bundle, as well as the one-sided growth of the endosperm tissue. The constriction existing between the haustorium and endosperm tissue is comparatively wide, with the result that the cytoplasm of the haustorium comes in contact with the endosperm tissue to a greater extent than in any other species examined.

Leonurus cardiaca.

Leonurus has a large haustorium with a contour much like that of *Stachys* (fig. 9). The haustorial nuclei have a more or less fixed position in that portion lying nearest the endosperm tissue. This is the reverse of the condition in *Stachys*, where the nuclei lie in the micropylar region. Their number varies from four to six. The definite position of the haustorial nuclei would suggest the presence of cell walls, but there was no evidence of them.

Leonurus bears a close resemblance to *Phrysostegia* in the proximity of the antipodal canal to the haustorium. The canal does not appear in the section shown in figure 9, so its position is indicated by the dotted lines. The lower portion of the endosperm tissue and its connection with the vascular bundle through the canal is shown in figure 10.

Brunella vulgaris.

This species possesses a large cœnocytic haustorium containing nuclei without definite position. In this respect it is like *Lamium*. The antipodal haustorial canal becomes laterally placed, but, unlike the two previously described genera, it remains near the base of the endosperm tissue.

The five genera thus far mentioned belong to the tribe Stachydeæ. No marked variations occur; in fact, they are

much more nearly alike than they are different. *Phrysostegia* appears to be the most divergent, but such divergence is really trivial. All are characterized by a large micropylar haustorium—a feature, however, which it shares with representatives of other tribes.

Teucrium canadense.

A glance at the diagram shown in figure 11 will show the relative position and size of the different portions of the embryo sac. The most noticeable difference between this species and those previously described is the relatively small size of the haustorium. The failure of the haustorium to enlarge much is doubtless mainly due to its proxity to the end of the beak-like extremity of the integument. There is but little room for enlargement. The haustorium contains a few nuclei that do not form a tissue. Whether this organ is really functional or not is difficult to determine with certainty. At most its activity can be only very slight, otherwise the extremity of the integument would undergo dissolution. The endosperm nuclei which are found in it do not have the size nor the altered appearance seen so frequently in vigorously acting haustoria. It would appear from this that alteration in the haustorial nuclei is to some extent at least proportional to the activity of the organ to which they belong.

Pycnanthemum lanceolatum.

The general configuration of the embryo sac is much like that of *Lamium* (fig. 12). The cœnocytic haustorium attains a large size, with the result that most of the micropylar portion of the integument becomes absorbed. The constriction between haustorium and endosperm tissue is soon obliterated, so that the two lie contiguous over a considerable area. The suspensor is long, as in the previously mentioned species, but owing to the size of the haustorium most of its length is found within the limits of this structure.

Lycopus rubellus.

Lycopus rubellus, when contrasted with *Pycnanthemum*, which belongs to the same tribe, differs in two respects; the haustorium is small, and the constriction lying between it and the endosperm tissue is relatively long (fig. 13). The basal portion of the endosperm tissue extends in a beak-like process to the end of the vascular bundle. This process occupies the

position of the antipodal canal of previously described species. Its origin may be explained by a growth of the tissue into the canal, which it thus displaces. The haustorium contains but one or two nuclei with no formation of tissue.

Mentha canadensis.

The integument in this species is not extensive, yet there is a large cœnocytic haustorium present which closely resembles that of *Pycnanthemum.* Like *Pycnanthemum,* there is in *Mentha* an early obliteration of the canal connecting haustorium and endosperm tissue. *Lycopus,* on the other hand, represents the other extreme, in which the canal persists for a long time. *Pycnanthemum, Lycopus* and *Mentha* belong to the tribe Satureineæ.

Salvia azurea and *Salvia lanceolata.*

These two species will be considered together, as they present many points in common. As compared with the representatives of other genera, however, they show marked differences. In the first place, they are unique in having two haustorial outgrowths, one cœnocytic and one composed of ordinary endosperm tissue. In addition, there is a well-developed antipodal canal.

In order to follow better the development of the haustoria, it will be advantageous to examine the definitive embryo sac and consider some of the phenomena immediately following fertilization. The definitive embryo sac of *Salvia lanceolata* is shown in figure 14. It is short, and in comparison with the extensive integument is relatively insignificant (fig. 15). The shortness is the more noticeable when the amount of space occupied by the egg apparatus is taken into consideration. The embryo sac is filled with a reticulated cytoplasm, which is distinguished from that of *Lamium amplexicaule* and other species examined by the absence of vacuoles. The antipodals lie in the depression which marks the beginning of the canal to the vascular bundle. The small size of the embryo sac necessitates the proximity of the endosperm nucleus to the egg apparatus.

Fertilization is followed by a very *slight* elongation of the egg cell—a marked variation from the condition found in the species of other genera examined. The explanation for this difference lies in the fact that none of the space occupied by the definitive embryo sac is to be included in haustorium formation,

since elongation of the egg and suspensor is always for the purpose of removing the embryo from the sphere of haustorial activity. In *Lamium* approximately half of the sac becomes haustorium, and it is in view of this fact that the embryo is transferred for development to the antipodal region. The elongation of the suspensor in the majority of Labiatæ examined appears to terminate its function, for disintegration follows. In *Salvia,* on the contrary, there is reason to believe that it plays an important part in embryo nutrition. The cells composing it are short and relatively rich in plasmatic contents.

The first division of the endosperm nucleus results in the formation of a cell at the extreme antipodal end of the embryo sac. The wall cutting off this cell lies approximately in a plane at right angles to the long axis of the embryo and suspensor. The separating walls of cells produced in succeeding divisions are at first parallel to the first wall. The embryo is soon surrounded by endosperm tissue (fig. 16). One endosperm cell takes a position near the end of the suspensor for the purpose of entering directly into the formation of a haustorium. The growth of the endosperm tissue surrounding the embryo is greatest in a direction toward the upper part of the integument and approximately parallel with the vascular bundle. As a result, an endosperm process, cylindrical in shape, projects into the region where lies the most extensive portion of integument tissue (fig. 17). The outgrowth is evidently designed to reach the nutritive tissue remote from the main mass of endosperm. Functionally, it is a haustorium, differing principally from tissue-containing haustoria of certain other families of plants in the greater number of cells. Figure 17 shows a young haustorium of *Salvia lanceolata.* In its maturer stages, seen diagrammatically in figure 19, it is composed of much elongated cells. Such differentiation suggests conduction as a function. The elongated cells lie principally in the axis of the haustorium with their long axes parallel to that of the haustorium. The peripheral cells serve as digestive and absorptive cells, while those of the interior of the haustorium are conductive. The products of its activity are transferred to the main mass of endosperm which it thus serves as an absorbing organ.

The other haustorium is cœnocytic, and its activities are directly concerned with embryo nutrition through the suspensor. It is not a structure developed from the suspensor, though

it continues it, in a way, out into the integument. It recalls some of the haustorial outgrowths in the suspensor cells in certain Orchidaceæ[2] and Rubiaceæ.[3] In *Salvia lanceolata* two endosperm nuclei take part in haustorium formation; more than two in *Salvia azurea* (fig. 18). In both species one end of the haustorium completes the basal or proximal portion of the suspensor. In *Salvia lanceolata* more of the suspensor is surrounded than in *Salvia azurea*. In the former the suspensor becomes bent while in the latter it remains straight.

The haustorium grows outward through the integument, taking a direction nearly at right angles to that taken by the other haustoria. The purpose of the cœnocytic haustorium is to dissolve the integument cells surrounding it, but it is unique in communicating the products of its activity to the suspensor. Attention has already been called to the striking differences between the *Salvia* suspensors and those of the other Labiatæ examined. As the former take part in embryo nutrition their cells present an appearance betokening activity. Instead of losing their protoplasmic contents or undergoing dissolution, as in instances where excessive elongation takes place, the suspensor cells of *Salvia* are healthy appearing, resembling the endosperm cells in this respect not a little.

The cœnocytic haustorium does not attain the size of the one composed of tissue (fig. 19). As in similar haustoria previously described, the nuclei are larger than those of the endosperm tissue.

A canal, bent at nearly right angles, is formed between the endosperm and the vascular bundle. There appears to be no nucleus in it, but granular material resembling cytoplasm is found along the side walls and at the end. As the main body of endosperm pushes outward at the expense of the integument cells, the canal does not suffer for a time (fig. 20). Instead, the endosperm becomes laid down around its proximal end. This gives the appearance of the canal piercing the tissue. The canal forms a direct communication with the vascular bundle, serving probably as a conduction to the endosperm.

Monarda fistulosa.

This species is patterned after *Lamium* rather than after *Salvia*. There is a large cœnocytic micropylar haustorium which does not differ materially from that of *Lamium*. A few nuclei are present, though of a relatively smaller size. The

embryo sac is narrow and the suspensor is very long. There is no antipodal canal, but the endosperm tissue bends toward the terminus of the vascular bundle in the form of a process.

Nepeta cataria.

The haustorium of *Nepeta cataria* is cœnocytic, and contains four nuclei that occupy a more or less definite position at its base or near the place where the suspensor passes into the constriction (fig. 21). The haustorium is relatively small, containing much less than half the length of the suspensor.

Dracocephalum sp.

This varies from the other species of Labiatæ examined in the character of the outline of the endosperm tissue. In the other species this tissue enlarges quite uniformly, presenting a smooth or entire outline when sectioned. The outgrowths in *Dracocephalum* have no definite position or form and hence are not to be regarded as other than integral portions of the endosperm tissue and not haustoria (fig. 22). The haustorium is much elongated, as is the endosperm tissue. The embryo lies in the upper portion of the latter, being attached at the end of a very long suspensor.

Scutellaria parvula.

The bent embryo sac of *Scutellaria,* resulting in a bent embryo in the ripe seed, is of course well known to taxonomists. It conforms to the other species in Labiatæ in possessing a haustorium, but located, as it is, at the extreme tip of the ovule, its growth is greatly limited, so that it remains small (fig. 23). The endosperm is elongated and tapers at the base into a hook-like process whose end lies near the terminus of the vascular bundle.

DISCUSSION AND CONCLUSIONS.

In a large number of plants, especially those in which two integuments are present, the embryo sac assumes a somewhat elliptical or oval form in longitudinal section, with an approximately entire outline. The nutrition designed for growth of the endosperm may be absorbed fairly uniformly over the entire surface of the sac, or it may be absorbed more rapidly at one point than at other points, but in either case the elliptical or oval outline is maintained. If added organs mean increased specialization, then embryo sacs of the type just mentioned,

without special absorptive structures, may be regarded as a simpler, less differentiated, perhaps more nearly primitive, sort.

In some instances the innermost cell layer of integument, which borders on the nucellus or else on the embryo sac, is specialized into a digestive layer, whose activity is directed against the remaining integument for the benefit of the embryo sac. The name "tapetum" has been frequently applied to this layer, but its use is justified only on account of the nutritive function it performs. Goebel[4] proposes the term "epithelium" as a substitute. Three characteristics usually pertain to the epithelium: first, it remains intact for a longer period than the integumental layers adjacent; second, its cells become differentiated in form or contents from those of the remaining integument; third, it apparently exerts a digestive action. The digestive action is doubted by some, among whom is Schmid,[5] who ascribes a protective function to it. Since the species of Labiatæ herein described do not develop an epithelium, it is without the province of this discussion to do more than call attention to the fact that Schmid challenges the results obtained by the "Goebelische Schule," thus showing that the problem is open for further investigation.

The Labiatæ, in common with some other sympetalous families, depart from the type described for many plants having two integuments by differentiating haustoria. The haustorium implies increased absorptive activity in one portion of the embryo sac, but not necessarily cessation of the function elsewhere. Among the labiates studied, all (with the single exception of *Salvia*) have a micropylar haustorium of some sort. In most of the species it is a well-developed structure, exhibiting manifest activity as a nutritive organ. But in such species as *Scutellaria parvula, Teucrium canadense,* and *Lycopus rubellus,* it is of small size, and its usefulness may with safety be said to be either greatly reduced or else obsolete. Whether such a condition really represents actual reduction from a previously more highly developed state, or whether it is primitive in its nature, is a problem yet to be solved. The much elongated suspensor is here offered as evidence favoring the former view, since the purpose of elongation is believed to be the removal of the embryo from the region of the haustorium. Extraordinary length in proportion to the size of the haustorium

might therefore mean that shortening of the former did not accompany reduction in size of the latter. Conditions external to the embryo sac may have had something to do with haustorium reduction in such a species as *Scutellaria parvula*, where narrowing of the integument to a beak left but little tissue to be exploited.

The nuclei in the cœnocytic haustorium merit interest on account of the extraordinary size and appearance some of them attain. Such nuclei are found in other families where similar haustoria exist. They have been described by Balicka-Iwanowska,[6] Schmid[5] and others. That they are transformed endosperm nuclei is of course easy to observe. Knowing the kind of work the haustorium is called upon to do, one might expect increase in size, both of entire nucleus and also of nucleolus, on account of extraordinary nutritive function. The loss of power to divide accompanies the development of this function. According to Schmid,[5] the nuclei should be considered degenerate structures, whose condition has been produced by excessive nourishment, as is attested by loss of power to divide. Instances of like nature are not limited to embryo sacs, but occur in mycorrhiza and in animals. There is room for difference of opinion, however, as to the governing principle underlying such nuclear change. It is at least open to investigation whether the increase in size is a direct result of degeneration, due to unusually favorable conditions regarding food supply, or whether it is due to the added functional responsibility demanded of them by the haustorium. It is questionable whether either failure to undergo division or exceptional abundance of nutriment should be used as a test of degeneracy. As evidence against the latter view, attention is called to the normal appearance of the nuclei in the cellular haustorium in *Salvia* and those in the endosperm cells adjacent to a cœnocytic haustorium. Both are in very favorable condition as to food supply, yet there is no nuclear enlargement. It would appear that cœnocytic structure is conducive to such enlargement, but it cannot be merely a question of food supply. A difference is to be noted in the lack of cell walls, which in a tissue may possibly exert a limiting influence on increase of size in nuclei. Another difference is seen in the relatively small number of nuclei in a cœnocytic haustorium. It might be difficult to prove, however, that for this reason the work demanded of each

nucleus would be greater, though of course there is a possibility that it might be true.

Haustoria have either indefinite or more or less definite positions of their nuclei. Walls might be expected in instances where the nuclei are definitely placed. Balicka-Iwanowska[6] found a very delicate gelatinous membrane present in certain instances of this sort. No walls were evident, however, in any of the micropylar haustoria of the Labiatæ.

Indefinite location of nuclei are associated with irregular form of haustorium, while those having a more nearly fixed position are found in such as have an approximately symmetrical form.

The Labiatæ investigated generally have long suspensors, which are associated with the presence of micropylar haustoria. An exception is seen in *Salvia*, which has a short suspensor and no micropylar haustorium. The direct results of suspensor elongation are the removal of the embryo from the haustorium and its transfer to the vicinity of the center of the growing endosperm tissue. These results are doubtless sufficient to serve as causes for suspensor elongation. It is at least evident that a position within the haustorium would not be as favorable as a position without in so far as the products of haustorial activity are concerned. The endosperm tissue itself exerts a digestive action on the integument, and it also receives the nutriment from the haustorium, hence this tissue is more favorable for embryo development than the haustorium alone. Although integument cells are destroyed by the haustorium, there is no reason for believing that those of the embryo would likewise be, since endosperm tissue bordering on the haustorium is in no way affected by its digestive action. There is, therefore, no reason for thinking that suspensor elongation is to remove the embryo from the predatory action of the haustorium.

In general, it does not appear that the suspensor functions as a conductor of nutrition to the embryo. Evidence for this view is found in the collapsed condition of the suspensor through nearly its entire length, especially in that part lying within the haustorium. The greater portion of it is apparently without cell contents of any sort, and may or may not be continuous from the micropylar end of the embryo sac to the embryo. It would be expected of a cell or tissue that is serving

actively as a means of translocation of food materials that some vestige of life would be discernible. In *Salvia,* for instance, a healthy, vigorous condition of the suspensor cells accompanies activity in food transmission. In all the species examined (except *Salvia*), the only suspensor cells that appeared to be living were those immediately adjacent to the embryo. The nutrition of the embryo is accomplished through absorption over its entire surface, whereas in *Salvia* an added source of nutriment probably lies in the conducting power of the suspensor.

The length of the suspensor is roughly proportionate to the size of the haustorium through which the embryo has to be transported. Usually the movement is past a cœnocytic structure to a tissue. An instance is to be noted, however, in *Myoporum*[1] (Myoporaceæ), in which the growth is directly through one portion of the endosperm to another. The beaked portion of the endosperm is apparently a remnant of what may once have been a cœnocytic haustorium, but in which the cœnocytic condition has been lost.

The integument varies in thickness and extent in the different species. Of course, it is in those in which it is most extensive that the largest haustoria are possible. Through the integument in each case there runs a vascular bundle which terminates near the antipodal region. A slight outpocketing of the embryo sac is found extending into the integument toward the end of the bundle. Later it may develop into a canal without nuclei, or into a process of the endosperm. Its function in all cases is evident—to facilitate the passage of nutriment from the vascular bundle to the endosperm.

In summing up the characteristics that are common to the species described in this paper, with the exception of *Salvia,* they have been found to possess three that in the future may be shown to belong to the family as a whole. They are the micropylar haustorium, the much-elongated suspensor, and the antipodal canal or process. Marked variations from a common type, such as are found in *Salvia,* suggest a taxonomic rearrangement, even though the usual macroscopic characteristics resemble those of the family in which the varying species is placed. In a previous paper,[1] for instance, attention was called to the striking difference in the ovular structure of the Menyantheæ when compared with the coördinate subfamily

Gentianeæ. The two have since been raised to family rank, probably for other reasons, yet it is interesting to note that the structure of the ovule justified the wisdom of the change. In this way can a study of sporangial, gametophytic and embryonic structures be of service in establishing more natural relationships and groupings.

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